Getting variable xylem hydraulic resistance under control - interplay of structure and function

Getting variable xylem hydraulic resistance under control – interplay of structure and function.

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Running head: XYLEM HYDRAULIC RESISTANCE UNDER CONTROL

Over three decades ago, it was first observed that the hydraulic resistance of perfused stem segments of *Acer* twigs was significantly decreased when deionized water was accidentally replaced by tap water that contained a low concentration of metal ions (Zimmermann 1978). Initially, the effect of ions on xylem hydraulic resistance was seen as a methodological problem of limited biological importance rather than an evolved xylem trait (Sperry et al. 1988). The recognition that this phenomenon might substantially contribute to the regulation of water flow through plants came much later (van Ieperen et al. 2000; Zwieniecki et al. 2001). These reports challenged the classical paradigm of vessels being purely passive in water transport (Gartner 1995; Zimmermann 1983; Zimmermann and Milburn 1982). Recently, a new view has emerged: that these tubes can control/regulate sap flow in response to changing plant physiological status (Nardini et al. 2011; Zwieniecki et al. 2001). These follow-up studies were aimed at understanding the biophysical basis for the ion-mediated variable resistance of xylem and demonstrating the potential for a variable conductance in regulating water distribution in large dendritic structures that can help optimizing plant resource utilization or mitigate the effects of environmental perturbations (van Ieperen 2007).

The initial biophysical focus had a positive effect on refining our understanding of the central role that bordered pits play in plant water transport. It was proposed that porosity of the bordered pit membranes can be actuated by swelling/de-swelling activity of pectin based hydrogels that permeates the fibrous membrane structure (Zwieniecki et al. 2001). The role of hydrogel in the variable xylem resistance phenomen was indicated by combination of response to ion concetration, resposne to pH and resposne to non-polar solution (ethanol) all resulting in drop of bordered pit field resistnce. .However, the initial hypothesis that de-swelling opens micro channels in the bordered pit membrane (Zwieniecki et al. 2001; van Ieperen 2007) had to be

modified to reflect the recent results from direct observations of conformational changes of bordered pit structure using an atomic force microscope (AFM) (Lee et al. 2012). Lee and co-authors showed that while the general idea of hydrogels being responsible for the hydraulic properties of bordered pits did not change, the decrease of the membrane thickness is behind the decrease of the hydraulic resistance rather than change in membrane porosity. AFM analysis delivered a clear image of the change from an amorphous featureless surface of the membrane in DI water to a rigid sharp fibrous surface in 50 mMol KCl solution (Figure 1). No submicron pores were observed in the membrane suggesting that water flow occurs via a hydrated hydrogel matrix rather than through the pores between cellulose fibers (Figure 1). We feel that these recent findings clarified the basic understanding of the variable xylem resistance and allow for a re-focus from questions such as 'how does it happen?' to the analysis of the physiological role of the variable hydraulic resistance of xylem in plants (Holbrook et al. 2002; Trifilo et al. 2011; van Ieperen 2007; Zwieniecki et al. 2004).

There is no doubt that an ever growing dendritic structure of the tree requires an efficient water distribution system. It was shown that xylem distribution system is often optimized following Murray's law that aims at minimization of xylem resistance for a given investment in transport tissue (McCulloh et al. 2004; Sperry et al. 2008) or fractal geometry that allow for vascular design where resistance is independent from path length (West et al. 1999). Once in place, this transport path remains active throughout the season without the possibility for structural changes. However, tree micro-environment is not constant. It undergoes continuous variations at multiple temporal scales from minutes (sun flecks, wind gusts) and hours (direction of sunlight) to days (drought, temperature) and weeks (competition, growth). Thus, an inflexible transport system acting in the variable environment may be temporarily inefficient causing a

drop in photosynthetic activity and possibly more permanent losses to transport functionality (embolism). The notion that xylem resistance is variable and can be controlled by both plant physiological activity and potentially by environmental conditions could make the xylem distribution system more robust and efficient. In this issue of Tree Physiology, Nardini and colleagues unequivocally show that the degree of variability of xylem hydraulic properties in response to ion concentration in xylem sap is correlated with plant habitat even among closely related species (Nardini et al. 2012). They reported that trees growing in shady and humid areas, with generally low evaporative demand and limited temporal/spatial variability in transpiration rates experienced by different parts of the tree crown, showed smaller variation in resistance to changes to ion concentration. This was in contrast to a greater ion-mediated hydraulic response in the trees growing in open areas with high sun exposure, high evaporative demand and potential for high variation in transpiration rates among different parts of the crown. The differences in responsiveness to changes in ion concentration seemed to be further supported by the fact that species growing in open environments have generally lower ion concentrations in xylem sap and that they operate in the range of concentrations where hydrogels are more responsive. This study suggests that the ionic response of xylem resistance is an evolved trait and can provide competitive or survival advantage related to water transport. Nardini and colleagues elegantly showed that the original hypothesis that 'ion-dependent mechanism for altering the hydraulic resistance of the xylem could allow plants to compensate for increases in resistance due to cavitation' (Zwieniecki et al. 2001) may indeed be supported by their data collected from *Acer* trees.

The crucial role that the structure of bordered pit membranes may play in the transport of water by providing protection from embolisms spreading (Plavcova et al. 2011; Sperry et al.

2006; Trifilo et al. 2008) should be extended to include their role in control of water fluxes. This warrants more thorough studies of the evolution of bordered pit membranes, their chemistry and most importantly their detailed anatomy in relation to ion response. Analysis of pectin distribution in fossilized plants suggests that evolution of bordered pit membranes responsivness to ion concentration might be present in multiple lines with angiosperms being most responsive due to high concentration of pectin like material (Boyce et al. 2004). In addition, the fact that changes of membrane thickness are the basis for the hydraulic response can help to understand differences between species response, with *Laurus nobilis* showing one of the highest recorded responses (Zwieniecki et al. 2001) and having one of the highest recorded thicknesses of the membrane (Jansen et al. 2009). As thicker membranes also provide better protection from embolism spread, there is a striking link between membrane functions: protection and flow control. Yet despite the research progress and growing interest, we still know very little on the true role of the ionic effect at the whole plant level with many unsolved questions regarding its role in nutrient management, resource distribution and transport optimization.

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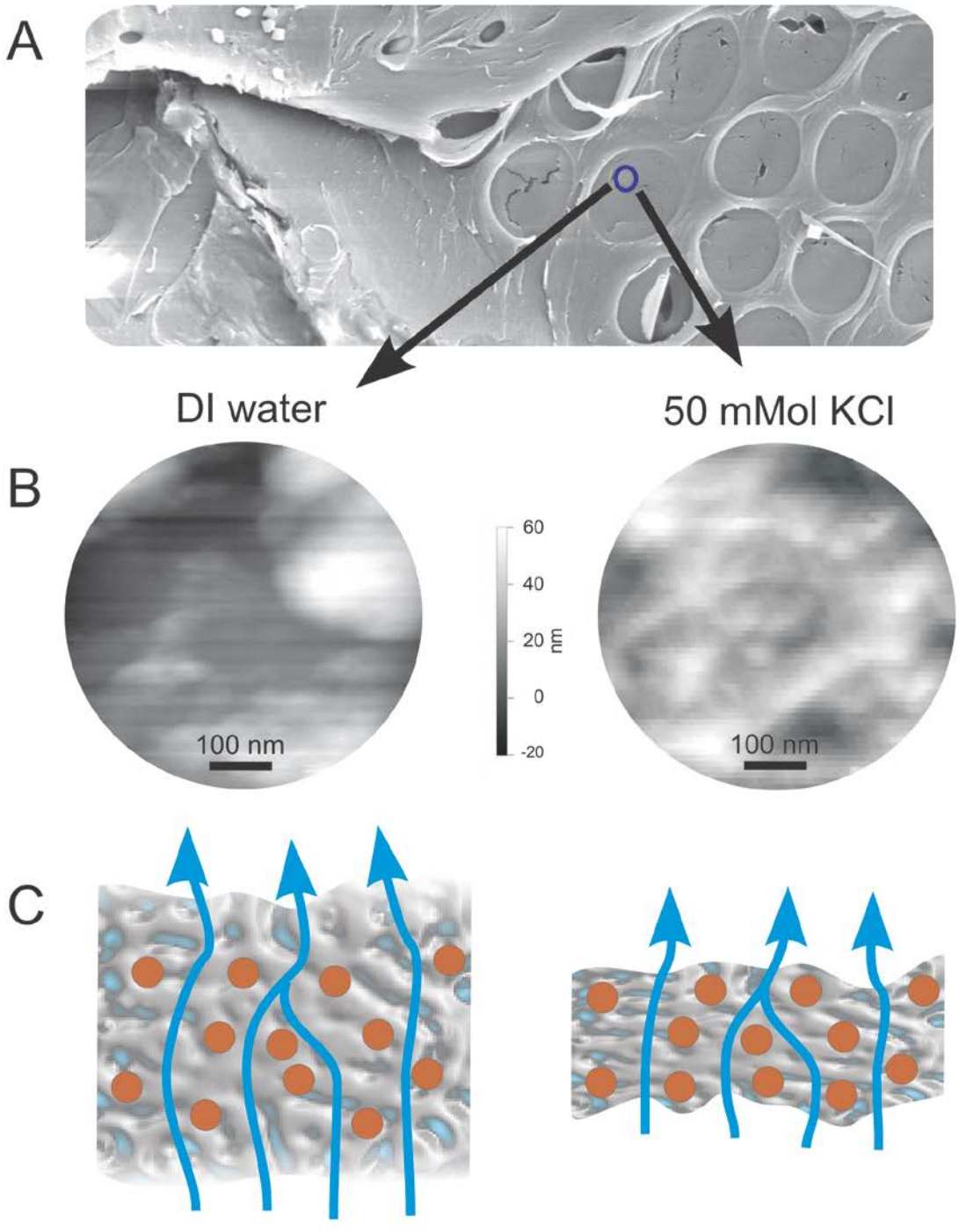
Figures

Figure 1. Current model describing the role of hydrogels in variable resistance of bordered pit membrane in response to changes in ion concentration. (A) Scanning electron microscope image of bordered pit field between adjacent vessels in *Nicotiana tabacum*. (B) Atomic force microscope (AFM) images depicting bordered pit field membrane surface that was initially submerged in deionized water (DI) and later switched to 50 mMol KCl solution (same exact region). Dramatic change from cloudy, featureless surface in DI water to sharp edges and visible fibrous structures can be observed (Lee et al. 2012). In addition, membrane was found to collapse in thickness upon switch from DI water to solution as the AFM cantilever had to be lowered several tens of nanometers to a new position to acquire new image. Shades of gray surface elevation (bar). (C) Schematics of the membrane cross section depicting current understanding of the hydrogel role in variable resistance of the xylem in response to ion concentration. Cellulose microfibers are imbedded in pectin hydrogel and water flows through the hydrogel matrix. Upon change from DI water or low ion concentration to solution with higher ion concentration, hydrogel matrix collapses decreasing the membrane thickness vertical distance between fibers and overall resistance of the path through the membrane (as resistance is inversely related to distance).



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